

CALCARATLOBELIA (CAMPANULACEAE): A NEW GENUS OF SPURRED LOBELIOIDS FROM MEXICO AND CENTRAL AMERICA

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ABSTRACT

The case is presented for the recognition of two genera of spurred lobelioids, *Heterotoma* and *Calcaratolobelia*, both presumably derived from the genus *Lobelia*. Formerly both genera were included in the genus *Heterotoma* Zucc. by most authors. Ayers (1990) concluded, however, that the spurred, blue- or pink-flowered lobelioids ought instead to be included within *Lobelia* section *Hemipogon* Benth. & Hook. A key and descriptions distinguishing the two spurred genera derived from the genus *Lobelia*, i.e. *Heterotoma* Zucc. and *Calcaratolobelia* Wilbur gen. nov., are provided together with the needed combinations with the synonymy of the twelve species and one variety that form the genus *Calcaratolobelia*: *C. aurita* (Brandege) Wilbur, *C. cordifolia* (Hook. & Arn.) Wilbur, *C. flexuosa* (C. Presl) Wilbur, *C. flexuosa* var. *intermedia* (Hemsley) Wilbur, *C. gibbosa* (S. Watson) Wilbur, *C. goldmanii* (Fern.) Wilbur, *C. knoblochii* (Ayers) Wilbur, *C. macrocentron* (Benth.) Wilbur, *C. mcvaughii* (Ayers) Wilbur, *C. margarita* (F. Wimmer) Wilbur, *C. pringlei* (B.L. Robinson) Wilbur, *C. tenella* (Turcz.) Wilbur, and *C. villaregalis* (Ayers) Wilbur. The synonymy of each taxa forming the genus *Heterotoma* is also provided.

RESUMEN

Se pretenden reconocer dos géneros lobeioides con flores espolonadas, *Heterotoma* y *Calcaratolobelia*, ambos probablemente derivados del género *Lobelia*. Anteriormente la mayoría de los autores incluían ambos géneros en *Heterotoma* Zucc. Ayers (1990) concluyó, sin embargo, que las lobeioides, de flores espolonadas azules o rosadas deberían incluirse en *Lobelia* sección *Hemipogon* Benth. & Hook. Se ofrecen una clave y descripciones para distinguir los dos géneros de flores espolonadas derivados del género *Lobelia*: *Heterotoma* Zucc. y *Calcaratolobelia* Wilbur gen. nov., junto con las combinaciones necesarias con las sinonimias de las doce especies y una variedad que forman el género *Calcaratolobelia*: *C. aurita* (Brandege) Wilbur, *C. cordifolia* (Hook. & Arn.) Wilbur, *C. flexuosa* (C. Presl) Wilbur, *C. flexuosa* var. *intermedia* (Hemsley) Wilbur, *C. gibbosa* (S. Watson) Wilbur, *C. goldmanii* (Fern.) Wilbur, *C. knoblochii* (Ayers) Wilbur, *C. macrocentron* (Benth.) Wilbur, *C. mcvaughii* (Ayers) Wilbur, *C. margarita* (F. Wimmer) Wilbur, *C. pringlei* (B.L. Robinson) Wilbur, *C. tenella* (Turcz.) Wilbur, y *C. villaregalis* (Ayers) Wilbur. También se ofrece la sinonimia de los taxa que forman el género *Heterotoma*.

My introduction to the lobelioid genus *Heterotoma* (Campanulaceae: Lobelioideae) was in the early spring of 1948. It was in the old National Herbarium of Mexico then located in Chapultepec Park in Mexico City.

Rogers McVaugh, whose assistant I had the great good fortune to be on his first trip to Mexico, was paying a courtesy call on its then Director, Maximiliano Martínez. Dr. Martínez, whose English was said to be excellent, kept that fact from us. Dr. McVaugh spent a difficult afternoon of one day and the morning of another struggling to express himself in Spanish with very little help and no evidence of sympathy from Dr. Martínez. I soon escaped the linguistic ordeal by wandering off to browse in the herbarium. Afterwards I commented on the extreme heterogeneity of *Heterotoma* as clearly demonstrated by the collections. Dr. McVaugh indicated that the genus was not very natural, in that one species, *H. lobelioides*, seemed to be derived from the genus *Lobelia* in the vicinity of *Lobelia laxiflora*, and the small-, and blue-flowered species of *Heterotoma* more closely resembled the numerous blue-flowered *Lobelias*. The hypanthial spur was the principal feature binding together the disparate species composing *Heterotoma*. McVaugh commented that this was not an ideal example of a natural genus but perhaps it was the best that could be done with what was in all probability merely "a genus of convenience." This appraisal was later reaffirmed by him (1965), noting that taxonomy would not "be well served" by the addition to *Heterotoma*, of a very different spurred species of *Lobelia* from Colombia. Pragmatic treatments such as this may have served us well in mid-century and for a few decades thereafter, but their chances for continued unchallenged acceptance in the age of cladism is slight.

McVaugh's (1940) study of the problems of generic recognition within the lobelioids led him to the following generalizations:

"It appears, then, that almost any attempt at a natural classification of the Lobelioideae must strike a balance among the following courses: (1) Define a considerable number of small genera, each fairly uniform in character, but set off from closely related groups by purely arbitrary characters. This course involves the creation of a number of new names. (2) Make generic limits ample enough to allow for the inclusion of most of the anomalous species. This will tend to make the genera larger and fewer, and will also necessitate the creation of many new names. (3) Make the genera as small and homogeneous as is compatible with logic, at the same time recognizing the weight of convention as it bears on the subject of generic limits. It seems to me [i.e., McVaugh] that best results may be obtained from this last course, if at the same time it be remembered that the 'genus', as ordinarily defined, is a conventional concept; it is less a natural unit than the species and more to be thought of as a means of classification. Convenience, therefore must be taken into account as well as apparent kinship between species or groups."

Ayers (1990), having investigated the species comprised in the traditional genus *Heterotoma* and its presumed closest relatives, concluded that

her admittedly “abbreviated study ... supports the hypothesis of parallel evolution of nectar spurs in at least two separate lineages within the Mexican and Central American members of *Lobelia*” and “makes the recognition of the polyphyletic genus *Heterotoma* untenable”

Some may recall the “good old days” when Simpson’s definition (1961, p.124) that monophyly “is the derivation of a taxon through one or more lineages ... from one immediately ancestral taxon of the same or lower rank,” was thought adequate. Under such a concept of monophyly, it would seem that even *Heterotoma* in the traditional sense would be considered monophyletic, because the red and yellow, large-flowered *Heterotoma lobelioides* is suspected of having been derived from *Lobelia* section *Homochilus* A.DC., while the pink, white or bluish, small-flowered species may well have evolved from *Lobelia* section *Hemipogon* Benth. & Hook. f. In this event, the genus *Heterotoma* in its entirety would be thought to have evolved from the genus *Lobelia*, an ancestral taxon of the same rank. This of course is contrary to Hennigian principles since the “stem” *Heterotoma* is by inference a *Lobelia*.

Although not convinced that *Heterotoma* in the sense of McVaugh (1943) and Wimmer (1953) and other pre-Hennigian authors has been demonstrated to be unacceptably “polyphyletic” as claimed by Ayers, at least as the term was used in the first half of the century, it must be conceded that times have changed and that a stricter and narrower interpretation is now the prevailing practice in delimiting genera. If *Heterotoma*, in the restrictive sense of the original publication and of Ayers’ (1990) conclusion, is deemed worthy of generic status, at least until further studies are completed, it would seem that the spurred, small-flowered derivatives of *Lobelia* are equally deserving of generic recognition.

Ayers concluded emphatically that the generic independence of *Heterotoma* s.l. (including both the red-yellow flowered species (*H. lobelioides*) and the blue-flowered species) was unacceptable. Ayers stated that there were three acceptable alternatives to the scheme she favored.

- 1) Place all species of *Heterotoma* in the appropriate sections of the *Lobelia* from which they apparently evolved i.e. place the blue or pink flowered species in *Lobelia* sect. *Hemipogon* and the red & yellow, long-spurred species in *Lobelia* section *Homochilus*.
- 2) Retain *Heterotoma lobelioides* as a separate monotypic genus and recognize the two groups of small-flowered species as members of the paraphyletic genus *Lobelia*.
- 3) Recognize a monotypic *Heterotoma lobelioides* with its two varieties and establish a new genus for the two small-flowered species groups, *Macrocentron* and *Cordifolia*.
- 4) Transfer *Lobelia margarita* to a newly erected genus containing the members of *Heterotoma*, excluding *H. lobelioides*.

Ayers considered the fourth alternative acceptable only if evidence in addition to the presence of floral spurs could be found relating *Heterotoma pringlei* and the very similar, pouched but non-spurred *Lobelia margarita* to the small-spurred taxa. It would seem to me that if Ayers' investigation demonstrated anything convincingly it was that *margarita* and *pringlei* are closely related.

The establishment of a new genus for the small-spurred, blue-flowered species, although admittedly theoretically justifiable, was not favored by Ayers, fearing the proliferation of small, even though monophyletic, genera. Ayers favored the second of the listed options even though her solution continued recognition of a paraphyletic *Lobelia*. Because she could not demonstrate that *Lobelia laxiflora* is a sister "group" to the small, blue-flowered herbaceous species of *Lobelia*, Ayers concluded that it would be premature to transfer *Heterotoma lobelioides* into *Lobelia* section *Homochilus* since such a change might prove superfluous after the "final" analysis of *Lobelia* is completed.

My sense of logical order within the spurred lobelioids leads me to favor the fourth alternative listed by Ayers: namely the recognition of *Heterotoma* as one genus probably derived from *Lobelia* in the vicinity of section *Homochilus* A.DC. and the establishment of a new genus for the bluish or pink-flowered spurred (or at least pouched) species apparently also derived from *Lobelia* but from section *Hemipogon* Benth. & Hook. f.. Cladists will condemn both Ayers' arrangement and mine. The genus *Lobelia* is admittedly rendered paraphyletic in Ayers treatment; cladistically my arrangement is even less tolerable since in all likelihood both *Heteropogon* and *Calcaratolobelia* are derived from different sections of *Lobelia* and hence *Lobelia* is in all likelihood twice paraphyletic. (Perhaps one should leave well enough alone, but surely more trouble is in the offing for *Lobelia* and the stability of classification in the Lobelioideae. There would seem to be no possibility of maintaining *Diastatea* Scheidw. as a genus distinct from *Lobelia* if the same criteria are applied to it as have been to the small-spurred species here referred to *Calcaratolobelia*.)

McVaugh (1945, p. 15–17) presented a series of eight recommendations to serve as a formal set of generic criteria for the Campanulinae, with which he was then primarily concerned, but which have proved helpful in other families. Two of his recommendations perhaps offer guidance (and support) for the course of action taken here:

"Recommendation 3 ... Genera of the nature of satellites, if also comprising two or more series of species, invite suspicion especially if united by a single character which is also the only character separating them from a more inclusive genus."

This recommendation would argue against the recognition of *Heterotoma* s.l. since it comprised two or more series of species, the red and yellow, large flowered *H. lobelioides* and the blue and white or pink, small-flowered

species as both series are united by a single character (i.e. the nectariferous spur) which is “also the only character separating them from a more inclusive genus” [i.e., *Lobelia*].

Recommendation 6. “Any segregate genus should be sharply delimited; that is, any species which is *intermediate* in one or more respects towards a more inclusive genus should be relegated to the latter. The retention of the anomalous species in the more inclusive genus will change its limits, if at all, but very slightly, and only in this way can the segregate genus be precisely defined.”

This recommendation would support Wimmer’s original placement of *Heterotoma pringlei* (= *Lobelia gypsophila* Ayers) in the genus *Heterotoma* rather than in *Lobelia*, where Ayers placed it, but to say this is not fair to Ayers for she placed all of the bluish or pinkish to white-flowered species in the genus *Lobelia*. It was her firm conviction that the spurred *Heterotoma pringlei* is not only a *Lobelia* but that it is more closely related to the pouched but non-spurred *Lobelia margarita* than it is to any of the other bluish or pinkish, small-flowered, spurred species as shown by its gypsophilous soil preference, pedicellary movements during fruit maturation, similar and unique pollen exine, and similar, somewhat smaller, unusually colored seeds. Acknowledging the close relationship between *Heterotoma pringlei* (= *Lobelia gypsophila*) and *Lobelia margarita* as demonstrated by the shared features listed above, it would seem best to place the two species in one genus. Ayers concluded “that despite the difference in hypanthial morphology, they should not be placed in separate genera” and the genus to which both were assigned by her was *Lobelia*.

In contrast I place both of these species (i.e. the species that Ayers refers to as *Lobelia margarita* F.E. Wimmer and *Lobelia gypsophila* Ayers (= *Heterotoma pringlei* B.L. Robinson) together with both groups of spurred “lobelioids” that Ayers designated as the “*cordifolia* species groups” and the “*macrocentron* species group” into the same new genus here designated as *Calcaratolobelia*. These three species groups can be separated by the following key.

1. Decumbent or procumbent perennial herbs spreading from underground rhizomes; pedicels erect and stationary during fruit maturation; corolla pinkish purple A) the **Macrocentron** species group.
1. Erect annual herbs or tap-rooted perennials; capsule reoriented during fruit maturation by movement of the pedicel; corollas blue, pale lavender or white or rarely pink-purple.
 2. Tap-rooted perennials; pedicels divergent at 90° angles, in fruit deflexing abruptly at the hypanthium and reorienting the capsule, with spur or pouchside down and nearest the stem axis B) the **Gypsophila** species group.
 2. Fibrous-rooted or tap-rooted annuals; pedicels arcuate at 45° angles, in fruit reflexing abruptly at the hypanthium and reorienting the capsule, with the spur-side nearest the stem axis C) the **Cordifolia** species group.

This is Ayers' fourth alternative treatment of the possible relationships of the components of *Heterotoma s.l.* and their presumed ancestral groups within *Lobelia*. She did not favor this alternative until additional evidence besides the presence of floral spurs was found relating "*Heterotoma pringlei* (and thus *L. margarita*) to the other small-spurred taxa."

It is disconcerting that one is now placed in such a defensive position by recognizing segregate genera such as *Heterotoma* and *Calcaratolobelia*. Such segregates clearly render the very large genus *Lobelia* paraphyletic and therefore are unacceptable to a great many cladistically indoctrinated systematists. Brummitt (1996), in a most interesting defense of the unavoidability of paraphyletic taxa, urges us "not to be ashamed of paraphyletic taxa" as they are and have been "an unavoidable and essential feature of our taxonomy." Clearly, if the orthodox cladists are correct, we systematists have barely begun our tasks for an alarming percentage of genera and families currently recognized are paraphyletic (Funk 1985; Judd et al. 1994). If one's taxonomy admits that the evolutionary process has produced the incredible diversity which we attempt to classify, then it seems inevitable that a great many of our taxa will be demonstrably ancestor-descendantly related. Such groups conflict with the cladists concept of monophyly since the recognized group does not include all of its descendants i.e. in this case the genus *Lobelia* does not include two of its probable descendants, the segregate genera *Heterotoma* and *Calcaratolobelia*.

Perhaps brief comment is in order concerning the species described by McVaugh (1965) from the northern Andes of Colombia. McVaugh went to some pains to point out that, despite the gibbosity of the hypanthium, his new Columbian species clearly had nothing to do with the Mexican and Central American spurred *lobeliads* formerly placed in the genus *Heterotoma*; morphology suggested to McVaugh that the Andean species apparently was derived from *Lobelia* subg. *Tupa*.

KEY TO THE NORTH AMERICAN SPURRED OR POUCHED GENERA OF THE LOBELIOIDEAE

1. Floral spurs crescent shaped, inflated laterally, the tube narrowing distally and with an abruptly dilated base; corolla red and yellow; calyx lobes attached to the distal end of spur, appressed to corolla tissue **Heterotoma**
1. Floral spurs conical or cylindrical, not inflated laterally, the base not dilated; corolla white, lavender-blue, or pink-purple in spurred species; calyx lobes variously attached to the hypanthium, when distal at the sides of a cylindrical spur, then oriented at a 90° or greater angle from the spur axis... **Calcaratolobelia**

HETEROTOMA Zucc.

Heterotoma Zucc., Flora 15(2) (Beibl.):100. 1832. TYPE SPECIES: *H. lobelioides* Zucc.

Myopsia C. Presl, Prodr. Monogr. Lobel. 8. 1836. TYPE SPECIES: *Myopsia mexicana* C. Presl (= *H. lobelioides* Zucc.).

Perennial, suffrutescent herbs to 1.5 m tall. Leaves petiolate, ovate, pubescent, with acuminate apices, the margin with yellow or purple, gland-tipped teeth. Flowers resupinate by twisting of the ebracteolate pedicel. Hypanthium asymmetrical, the calyx and corolla elongated on the lower side into an arcuate, inflated spur with a bulbous base. Corolla unilabiate, the spur with all 5 lobes on the apparent abaxial side and pointing downward, the tube slit dorsally to base; tube and spur yellow-orange to burgundy; lobes subulate, yellow. Staminal column ca. 2 cm long, exerted vertically from dorsal slit in corolla; ventral filaments adnate to hypanthial rim and continuous with it to base of spur; ventral anthers with many, stiff, subulate trichomes at apex. Corolla, stamens, and style persistent on the fruit. Fruit capsular, dehiscent by apical valves. Seeds numerous (60–100/capsule), ellipsoid, 0.55–0.6 mm long. $n=7$.

1a. *Heterotoma lobelioides* Zucc. var. *lobelioides*, Flora 15(2)(Beibl.):101. 1832. TYPE: MEXICO. OAXACA(?): La Cumbre de San Antonio, 8000 ft, no date, *Karwinski s.n.* (HOLOTYPE: M; ISOTYPES: JE, M, W).

Myopsia mexicana C. Presl, Prodr. Monogr. Lobel. 8. 1836. TYPE: MEXICO. OAXACA(?): La Cumbre de San Antonio, 8000 ft, no date, *Karwinski s.n.* (NEOTYPE: ?).

Lobelia calcarata Bertoloni, Fl. Guatimal. in Novi. Comment. Acad. Sci. Inst. Bononiensis 4:409. 1840. TYPE: GUATEMALA: Pinula, 4200 ft, *J. Donnell Smith* 1925 (NEOTYPE: NY, designated by Ayers 1990).

Heterotoma tonelii Ortgies, in Regel, Gartenflora 12:50. 1863. TYPE: illustration in van Houtte, Fl. Serres 14: pl. 1454. 1863 (LECTOTYPE, designated by Ayers 1990). *H. lobelioides* var. *tonelii* (Ortgies) F. Wimmer, Ann. Naturhist. Mus. Wien. 56:371. 1948.

1b. *Heterotoma lobelioides* Zucc. var. *glabra* Ayers, Syst. Bot. 15:311. 1990. TYPE: MEXICO. SAN LUIS POTOSÍ: in mountains near Santa María del Río, Aug 1876, *Schaffner* 736 (HOLOTYPE: GH; ISOTYPE: US).

CALCARATOLOBELIA

Calcaratolobelia gen. nov. TYPE: *Calcaratolobelia cordifolia* (Hook. & Arn.) Wilbur (= *Lobelia cordifolia* Hook. & Arn.).

Herbae annuae vel perennes. Pedicelli graciles, saepe ebracteolati vel raro infimo cum bracteolis minutis et filiformibus. Hypanthia infirme ad valde asymmetrica, partim in calcari corollae distenta, irregularia. Corolla tubulosa, in uno latere longitudinaliter fissa, basi in calcari plus minusve longum extensa vel solum *gibbosa*; limbus corollae bilabiatus, quinquepartitus. Filamenta a corolla libera, sed duo longiora et in apicem calcaris decurrentia. Antherae 2 minores apice piloso-penicellatae. Stylus filiformis inclusus. Capsula semi-infera.

Annual or perennial herbs (1–)10–70(–150) cm tall. Leaves petiolate or the cauline sometimes sessile. Inflorescences often secund and appearing pedunculate due to the naked upper part of the stem. Pedicels spreading-

ascendent, slender, often ebracteolate or in two species with minute, filiform bracteoles especially on the lowermost pedicels. Flowers inverted in anthesis by the twisting of the pedicel. Hypanthium weakly to strongly asymmetrical, the calyx and corolla extending on the abaxial side into a nectariferous knob or spur, the spur straight, cylindrical or tapering or at least not possessing a bulbous base. Corollas bilabiate with the two upper and three lower lobes, respectively, pointing in opposite directions, the tube slit dorsally to base or at least to within 1 mm of base. Staminal column less than 8 mm long and slightly exerted through the dorsal slit; the 2 shorter anthers with a stubble of numerous, short, apical bristles. $n=7$ or 14 when known.

A small genus of twelve species known only from Mexico and Central America.

Ayers' (1990) key and descriptions adequately summarize the differences between the species and it seems unlikely that they can be improved upon until considerably more material has been collected and evaluated. The revised nomenclature is presented below with the species arranged in the same order as in Ayers' publication except for the insertion of *L. margarita* as species #12.

1. **Calcaratolobelia macrocentron** (Benth.) Wilbur, comb. nov. *Heterotoma macrocentron* Benth., Hooker's Icon. Pl. 12: 68, pl. 1177. 1876. *Lobelia macrocentron* (Benth.) Ayers, Brittonia 39:418. 1987. TYPE: MEXICO. [DURANGO or NAYARIT?]: Sierra Madre, NW of Mexico, Nov–Feb 1849–50, *Seemann* 2049 (HOLOTYPE: K; ISOTYPE: BM).
 2. **Calcaratolobelia villaregalis** (Ayers) Wilbur, comb. nov. *Lobelia villaregalis* Ayers, Brittonia 39:419. 1987. TYPE: MEXICO. JALISCO: cañon humido, Sierra de La Venta, 24 Nov. 1968, *Villareal de Puga* 2463 (HOLOTYPE: MICH; ISOTYPE: IBUG).
 3. **Calcaratolobelia knoblochii** (Ayers) Wilbur, comb. nov. *Lobelia knoblochii* Ayers, Brittonia 39:420. 1987. TYPE: MEXICO. CHIHUAHUA: shaded rocks, Mojarachic, 25 May 1938, *Knobloch* 5097 (HOLOTYPE: F; ISOTYPE: MSC).
 4. **Calcaratolobelia mcvaughii** (Ayers) Wilbur, comb. nov. *Lobelia mcvaughii* Ayers, Brittonia 39:421. 1987. TYPE: MEXICO. DURANGO: 34 road mi W of El Salto, along hwy from Durango to Mazatlán, 24 Mar 1951, *McVaugh* 11528 (HOLOTYPE: MICH; ISOTYPES: MICH, NY, TEX).
 5. **Calcaratolobelia cordifolia** (Hook. & Arn.) Wilbur, comb. nov. *Lobelia cordifolia* Hook. & Arn., Bot. Beechey Voy. 301. 1838. *Heterotoma cordifolia* (Hook. & Arn.) McVaugh, Bull. Torrey Bot. Club 67:143. 1940. TYPE: MEXICO. NAYARIT: vicinity of Tepic, Jan–Feb 1827, *Beechey s.n.* (HOLOTYPE: E; ISOTYPE: K).
- Heterotoma salvadorensis* F. Wimmer, Ann. Naturhist. Mus. Wien 56:371. 1948. TYPE: EL SALVADOR. San Salvador, no date, *Bernouli & Cario* 8 (HOLOTYPE: GOET; ISOTYPES: GOET, W).

6. **Calcaratolobelia tenella** (Turcz.) Wilbur, comb. nov. *Heterotoma tenella* Turcz., Bjull. Moskovsk. Obsc. Isp. Prir., Otd. Biol. 25(3):175. 1852. *Lobelia volcanica* Ayers, Syst. Bot. 15:317. 1990. TYPE: MEXICO. VERACRUZ: Xalapa, 600 m, Dec 1840, Galeotti 7029 (HOLOTYPE: K; ISOTYPE: BR). *Heterotoma cordifolia* var. *tenella* (Turcz.) F. Wimmer, Pflanzenr. IV. 276b:717. 1953, non *Lobelia tenella* L., Mantissa Pl. 1:120.1771, Thunb. Prodr. Fl. Cap. 40. 1794, non Biv., Sicul. Pl. Cent. 1:53.t.2. 1806.

7. **Calcaratolobelia gibbosa** (S. Watson) Wilbur, comb. nov. *Heterotoma gibbosa* S. Watson, Proc. Amer. Acad. Arts 23:280. 1888. TYPE: MEXICO. CHIHUAHUA: Oritz, no date, Pringle 1478 (HOLOTYPE: GH), non *Lobelia gibbosa* Labill., Nov. Holl. pl. 1:50. 1805.

Heterotoma endlichii F. Wimmer, Feddes Repert. Spec. Nov. Regni Veg. 26:1 pl.71, f.1. 1929. *Lobelia endlichii* (F. Wimmer) Ayers, Syst. Bot. 15:319. 1990. TYPE: MEXICO. CHIHUAHUA: bei Huejotitan in Tal des Río Balsequillo, 1720 m, 5 Apr 1906, Endlich 1172 (LECTOTYPE: W, designated by Ayers 1990).

8a. **Calcaratolobelia flexuosa** (C. Presl) Wilbur var. *flexuosa*, comb. nov. *Rapuntium flexuosum* C. Presl, Prodr. Monogr. Lobel. 23.1836. TYPE: MEXICO. presumably collected between Acapulco and Mexico City, no date, Haenke s.n. (HOLOTYPE: PR; photo: NY, US). non *Rapuntium flexuosum* C. Presl, Monogr. Lobel. 16.1836. TYPE: Cape of Good Hope. [*Rapuntium flexuosum* C. Presl (p. 23) has priority over *R. flexuosum* C. Presl (p. 16), see Art. 53. 6. ICBN. 1993.] *Lobelia flexuosa* (C. Presl) A.DC., Prodr. 7:378. 1839. *Heterotoma flexuosa* (C. Presl) McVaugh, Bull. Torrey Bot. Club 67:143. 1940.

Lobelia arabidoides Hook. & Arn., Bot. Beechey Voy. 301. pl. 66. 1838. *Heterotoma arabidoides* (Hook. & Arn.) Benth, Hooker's Icon. Pl. 12:68. 1876. TYPE: MEXICO. NAYARIT: vicinity of Tepic, Jan–Feb 1827, Beechey s.n. (HOLOTYPE: K).

Heterotoma flexuosa var. *liebmanniana* F. Wimmer, Pflanzenr. IV. 276b:718. 1953. TYPE: MEXICO. [Oaxaca?]: “San Miguel de Pueto, Guatala,” no date, Liebmann 7801 (LECTOTYPE, designated by Ayers (1990), who selected from among three syntypes: C).

8b. **Calcaratolobelia flexuosa** (C. Presl) Wilbur var. *intermedia* (Hemsley) Wilbur, comb. nov. *Heterotoma intermedia* Hemsl., Biol. Centr. Amer. Bot. 2:269.1881. *Heterotoma cordifolia* var. *intermedia* (Hemsley) F. Wimmer, Pflanzenr. IV. 276b:717. 1953. TYPE: MEXICO. [possibly collected between the cities of Durango and Tepic...]: 1850, Seemann 2051 (HOLOTYPE: K; ISOTYPE, BM).

9. **Calcaratolobelia goldmanii** (Fern.) Wilbur, comb.nov. *Heterotoma goldmanii* Fern., Proc. Amer. Acad. Arts 36:504.1901. *Lobelia goldmanii* (Fern.) Ayers, Syst. Bot. 15: 322. 1990. [as *goldmannii*]. TYPE: MEXICO. SINALOA: road from Las Flechas to La Rostra, 22 Feb 1899, Goldman 324 (HOLOTYPE: GH). [The spelling employed by Fernald, *H. goldmanii*, was altered by Wimmer to *H. goldmannii* (Pflanzenr. IV 276b:715–716. 1953), and this spelling was sometimes adopted by Ayers. The original collector's name was Edward A. Goldman but Wimmer mistakenly cited the collector's name as Goldmann. Article 60 applies; the original spelling must be retained.]

10. **Calcaratolobelia aurita** (Brandege) Wilbur, comb.nov. *Heterotoma aurita* Brandege, Proc. Calif. Acad. Sci. II. 3:149. 1891. *Lobelia aurita* (Brandege) Ayers,

Syst. Bot. 15:324. 1990. TYPE: MEXICO. BAJA CALIFORNIA DEL SUR: Sierra la Laguna, 21 Jun 1890, *Brandege* 353 (LECTOTYPE: UC, ISOLECTOTYPE: GH).

Lobelia cotensis M.E. Jones, Contr. W. Bot. 15:152. 1929. TYPE: MEXICO. BAJA CALIFORNIA DEL SUR: Cota Ranch, Laguna Mts, 14 mi E of Todos Santos, 21 Feb 1928, *Jones* 24147 (HOLOTYPE: POM, photo at US; ISOTYPES: F, MICH, MO, NY, POM).

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Nothing in this paper should be taken as criticism of Dr. Ayer's admirable contribution which is clearly based on her very careful study with its attention to field work especially in the mountains of Nuevo León. Quite obviously and admittedly my proposed solution is largely one that she listed as an "acceptable" alternative to the one that she prefers.

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